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REGULAR ARTICLE

Optimizing the choice of service crops in vineyards to achieve both runoff mitigation and water provisioning for grapevine: a trait-based approach

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Abstract

Aims In vineyards, service crops may increase water infiltration and positively contribute to soil water refilling, but may also increase the risk of competition for water with grapevines which could impair grape yield over several years. This study aimed to test the relationships between service crop functional traits and two related services of major interest in viticulture: runoff control and water provisioning.

Methods We measured the water stock, the cover rate, along with above- and belowground functional markers of 38 plant communities after a winter growing season in an experimental vineyard, to assess relationships between service crop functional markers, runoff control and water provisioning.

Results Both aboveground and belowground functional markers were significant predictors of service provision at the community level. The plant aboveground dry matter content was positively related to soil water stocks and negatively related to the cover rate of the communities, while the specific leaf area (SLA) was positively related to the cover rate. The rooting depth and morphological root traits (specific root length and very fine root fraction) were negatively related with the soil water stock. Moreover, these results agree with ecological theories about the relationships between plant functional markers, plant ecological strategies and resources use.

Conclusions The identification of functional markers related to service provision may help us to select species or communities service crops that could perform interesting trade-offs between multiple services due to a suited combination of related markers, and provide insights for plant selection in order to breed plant varieties and cultivars with the aim of providing agroecosystem services.

Highlights

- There is a trade-off between runoff mitigation and water provision in vineyards
- Trait-based approach allows to describe the functional diversity of service crops
- Service crops functional markers are related to runoff mitigation and water provision
- Trait-based approach is powerful to identify service crop functional profiles

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Keywords Trait-based approach · Cover crop · Ecosystem services · Runoff mitigation · Water provision · Vineyard soil management

Introduction

Water management is of particular importance in vineyards, whether for soil water replenishment during grapevines dormancy or efficient use of water resources during the grapevine cycle. On the one hand, rainfall often results in runoff and erosion in vineyards: grapevines do not cover the entire soil surface and are often planted on steep slopes where no other crop could grow, and frequent weeding can also exacerbate soil losses (Blavet et al. 2009; García-Ruiz 2010; Novara et al. 2018b). Controlling runoff also leads to an improved water infiltration and soil refilling, and water provisioning is of major importance in Mediterranean vineyards (Novara et al. 2018a). On the other hand, the time-course of water stress experienced by the grapevine from budburst to harvest needs to be managed effectively so as to ensure both quantity and quality of the berries (Pellegrino et al. 2006) and control vegetative development and the resulting disease incidence (Valdés-Gómez et al. 2011; Gaudin et al. 2014; Guilpart et al. 2017).

Service crops are crops grown to provide regulating and supporting ecosystem services to agriculture, primarily to do with soil fertility building or nutrient management, in contrast with the provisioning services of traditional marketed outputs such as food, fiber and fuel (Zhang et al. 2007; Garcia et al. 2018). It has been widely shown that service crops can help to control and decrease runoff and erosion in vineyards and positively contribute to soil water refilling (Celette et al. 2008; Gaudin et al. 2010), the vegetation cover being one of the most important factors influencing the rate of water infiltration (Durán-Zuazo and Rodríguez-Pleguezuelo 2008; Prosdocimi et al. 2016a). However, the soil cover needs to reach a particular threshold to efficiently mitigate runoff. Leonard and Andrieux (1998) observed that above a cover rate of 40%, the vegetation was dense enough to improve water infiltration and decrease runoff. In a review, Durán-Zuazo and Rodríguez-Pleguezuelo (2008) showed than from 20% cover, runoff volume can be reduced by half with the more consistent threshold being between 40 and 60% of soil cover. Snelder and Bryan (1995) showed that beyond 55% of vegetation cover soil losses were reduced by a factor of ten, while a threshold of 60% has been proposed to significantly reduce soil losses with mulching practices (Prosdocimi et al. 2016b, 2016c). However, growing service crops in vineyards may also increase the risk of competition for water between grapevines and service crops, which could impair grape yield over several years (Celette and Gary 2013; Guilpart et al. 2014, 2017). Several indicators can be used to assess the amount of water available for the grapevine through its growing season: the available soil water (ASW), i.e. the soil water content above the point at which plants experience a significant water stress, or the fraction of transpirable soil water (FTSW) which corresponds to the ratio between ASW and the total transpirable soil water (TTSW), i.e. the potential soil water accessible to the root system (Pellegrino et al. 2004, 2005). However, the optimum level of water stress during the grapevine cycle will depend on the wine produced and the desired berry quality and yield (Pellegrino et al. 2006; Gaudin et al. 2014). It is thus necessary to characterize the relationships between soil cover and water provision, and search for species or plant communities that balance both runoff mitigation and water provisioning (Novara et al. 2018a).

In order to scale up from species level to the functioning of plant communities we adopted comparative functional ecology (Lavorel and Grigulis 2012). Indeed, several authors have shown that comparative functional ecology may be a useful approach to optimizing ecosystem services in agriculture (Garnier and Navas 2012; Storkey et al. 2013, 2015; Damour et al. 2015; Martin and Isaac 2015). Comparative functional ecology makes it possible to compare species and plant community functions on the basis of plant traits whose measurement has been standardized (Pérez-Harguindeguy et al. 2013). Research has revealed general patterns of covariation between plant traits as consequences of differential resources use, which help to understand trade-offs between plant functions resulting to different ecological strategies, at both species and community scale (Wright et al. 2004; Westoby and Wright 2006; Pérez-Ramos et al. 2012; Díaz et al. 2016). Recently, Damour et al. (2018) proposed a revised “response/effect trait” framework for agroecosystems: response traits are used to describe how sown and spontaneous species respond to the filters of the agroecosystems, while effect traits are used to study how plants affect agroecosystem functioning (Lavorel and Garnier 2002). Thereafter, describing combinations of effect traits related to specific agroecosystem services (Damour et al. 2015; Storkey et al. 2015) may allow service crop “functional profiles” to be defined (Damour et al. 2014). Functionality could then be optimized by selecting a species with the requisite combination of traits or mixing species in a community (Storkey et al. 2015; Finney et al. 2017; Blesh 2018; Cresswell et al. 2019). Some studies have provided such species functional descriptions based on field experiments (e.g. Tardy et al. 2015; Wendling et al. 2016) or based on a combination of field experiment and modeling (Tribouillois et al. 2015a, 2015b). However, recent papers have highlighted the lack of studies that test the linkage between plant functional traits and ecosystem services in an agricultural context (Martin and Isaac 2015, 2018; Wood et al. 2015).

To significantly reduce runoff, we assumed that service crops should (i) have a fast juvenile growth and (ii) reach sufficient ground cover. The rate of plant establishment and soil cover can be assessed with the plant relative growth rate (RGR) (Damour et al. 2015). However, this trait is difficult to measure in field conditions, as it depends on localized soil conditions, making it difficult to compare measurements. Instead, the specific leaf area (SLA) is another relevant trait to assess the potential growth-rate of a species, as it is recognized as the main factor related to species photosynthetic capacity and thus relative growth rate variations among species (Westoby 1998; Lambers and Poorter 2004; Poorter and Garnier 2007; Damour et al. 2015). Moreover, this trait is widely used in trait-based studies applied to agroecosystems (Damour et al. 2014; Tardy et al. 2015; Tribouillois et al. 2015b; Wendling et al. 2016) as one of the fundamental traits of the leaf economics spectrum that summarizes variation in plant ecological strategies worldwide (Wright et al. 2004). The leaf dry matter content (LDMC) is complementary with SLA to determine plant strategies in resource acquisition and conservation (Wilson et al. 1999; Garnier et al. 2007). In addition, LDMC is related to leaf and litter fiber content, negatively related to litter decomposability, and is a relevant trait to assess the persistence of soil cover after destruction (Kazakou et al. 2006, 2009; Fortunel et al. 2009). The total dry matter content (DMC), corresponding to the dry matter content of the whole plant (leaves and stems), enables to assess the persistence of soil cover formed by mechanical destruction and not senescence. SLA, LDMC and DMC could also be used to assess the water provision service, as they relate to plant strategies that determine resource acquisition. Additionally, root traits were also measured as they are relevant to assess water consumption of plants (Reich et al. 2001; Barkaoui et al. 2016; Freschet and Roumet 2017; Fort et al. 2017). Moreover, roots may form zones of preferential flows for water infiltration, and may be related to a better soil water refilling in winter (Celette et al. 2008; Gaudin et al. 2010). Relationships between root traits and water acquisition have been highlighted in the literature at both species and community scale (Hernández et al. 2010; Pérès et al. 2013; Prieto et al. 2015; Freschet et al. 2015; Freschet and Roumet 2017; Fort et al. 2017). In this study, root length density (RLD), root mass density (RMD), specific root length (SRL), very fine root fraction (VFRf), root mass fraction (RMF) and root diameter were measured. Root diameter is negatively correlated to water acquisition, the other traits being positively correlated with water consumption (Freschet and Roumet 2017).

This study aimed to test the relationships between service crop functional traits and two related services of major interest in viticulture: runoff control and water provisioning. To assess the relationships between service crop functional traits and the two expected services, the functional structure (above- and belowground traits) of 38 plant communities was determined after a winter growing season in an experimental Mediterranean vineyard, along with the water stock and the cover rate of these plant communities. Plant communities were composed of monocultures of 13 contrasted service crop species that were sown in the inter-rows of the vineyard just after harvest, associated with the spontaneous vegetation that has developed with sown species. We hypothesized that i) the functional structure of plant communities is related to the indicators of service provision, and that these relations are consistent with the strategies expressed by plant communities through their functional structure (i.e. functional markers’ values). If so, the identification of favorable combinations of functional traits would allow optimal selection of service crops for the provision of agroecosystem services in vineyards to be identified (e.g. Blesh 2018).

Material and methods

Experimental site and design

The experiment was carried out on a vineyard located near Montpellier, south of France (43°31′55”N 3°51′51″

E), during the 2016–2017 crop cycle. The climate is Mediterranean with a cumulated rainfall of 479.5 mm from service crop sowing to data sampling (Fig. 1). Grapevines (*Vitis vinifera* L) were planted in 2008 with a density of 4000 stocks per hectare (2.5 m × 1 m), and consisted of two cultivars (cv. Mourvèdre and Grenache). Soil was a calcaric cambisol with 5% stoniness. Before starting the experiment, the experimental field had a legacy of three different soil management strategies (Table 1, Table S2), randomly located in the experimental field: some were tilled since 2012 (T), others had service crops each year since 2012 (SC), and some of the latter were tilled at year n-1 (SCT). In September 2016, inter-rows were sown with 13 service crop species after grapevines harvest and seedbed preparation, while bare soil was maintained under vine rows using mechanical weed control. In addition, another treatment composed of spontaneous vegetation was included in the experiment. Spontaneous vegetation treatment was also tilled as a seedbed preparation, but no sowings occurred and the vegetation emerged from the local soil seed bank. Soil texture was determined during the service crop growing period with 20 soil composite samples collected across the whole experiment (see Garcia et al. 2019). Mean percentages of clay, silt and sand were 27%, 39.5% and 33.5% respectively (Fig. S3).

The 13 different species of service crop selected for this experiment were chosen to represent a diversity of botanical families (Brassicaceae, Boraginaceae, Plantaginaceae, Rosaceae, Poaceae, Fabaceae), life cycles (perennial/annual), and growing habits (growth rate, biomass production, lifeform, flowering phenology), so as to maximize the range of functional trait values in the experiment. Chosen species were: *Achillea millefolium* (Am), *Brassica carinata* (Bc), *Dactylis glomerata* (Dg)*, Festuca ovina* (Fo)*, Medicago lupulina* (Ml)*, Medicago sativa* (Ms)*, Phacelia tanacetifolia* (Pt)*, Plantago coronopus* (Pc), *Poterium sanguisorba* (Sm), *Secale cereal* (Sc), *Trifolium fragiferum* (Tf), *Triticosecale* (Ts) and *Vicia villosa* (Vv). The 13 different species of service crop were sown on plots of 30 m length in each of the three previous soil management strategies. Plots represented an area covering one row and the two adjacent inter-rows, but only inter-rows were sown. Each service crop treatment was repeated in three plots. Emergence was low and delayed due to heavy rainfall that damaged the seedlings, and we couldn't maintain a balanced experimental design between the soil management strategies (see Table S1). No weeding was performed after sowing, so we obtained plant communities composed of sown and spontaneous species.

Plant functional characterization

One quadrat of 0.25 m^2 was placed in each of the plots before grapevines budburst, except for *Brassica carinata* (only one quadrat in the experiment), *Triticosecale* and *Secale cereale* (only two quadrats in the experiment), due to establishment failure. In total, we studied 35 quadrats composed of both the sown and spontaneous species (Table S1), and 3 quadrats composed of spontaneous vegetation only, for a total of 38 plant communities.

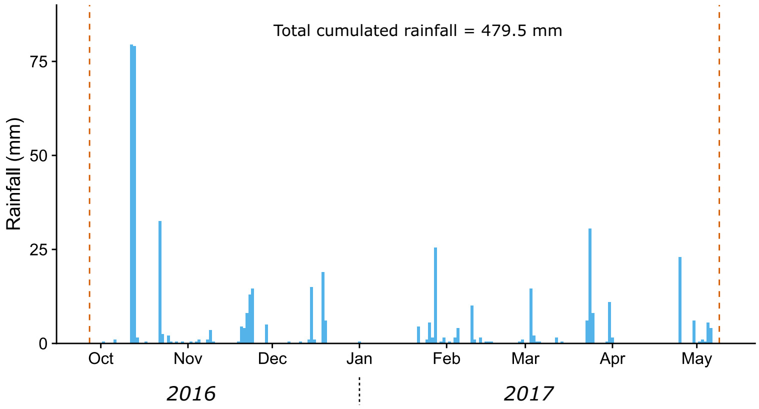
Aboveground vegetation sampling and trait measurements

At grapevines budburst (April 2017), all species (sown or spontaneous) were identified in each quadrat and their respective cover rate was estimated along with the total cover rate of the plant community. Then, total aboveground biomass was sampled from all quadrats. For each quadrat, species were separated and weighted separately after drying (72 h, 60 °C) to record their relative abundance in terms of aboveground biomass.

Aboveground traits were measured at grapevines budburst as well, only on species that represented 80% of the total biomass in each community (Pakeman and Quested 2007). 15 plants per species were collected in the inter-rows of the experiment for trait measurements, and all traits were measured according to standardized protocols (Pérez-Harguindeguy et al. 2013). Just after harvest, the plants were put in distilled water, and stored for the night at 5 °C for rehydration. After rehydration, leaf fresh biomass and total plant fresh biomass were measured. Leaves with petioles were scanned at 400 dpi with a scanner Epson Perfection V800, and leaf area was measured using WinFOLIA software (Regent Instruments, Quebec, Canada). Then, plants were oven dried at 60 °C during 72 h for dry weight determination. Dry matter content (DMC) was calculated by dividing fresh plant biomass by dry plant biomass. Leaf dry matter content (LDMC) was calculated by dividing dry leaf biomass by fresh leaf biomass. Specific leaf area (SLA) was calculated by dividing leaf area by dry leaf biomass.

To calculate functional markers at the community scale, we assumed that ecosystem function was

Fig. 1 Daily rainfall events during service crop growth (mm per day). Dashed lines represent sowing and destruction dates of the service crops



determined by the more dominant species in the community (the mass-ratio hypothesis, Grime 1998). Community-weighed means (CWM) were calculated for all traits following the equation:

$$CWM = \sum_{i=1}^{n} trait_i \times p_i \quad (1)$$

where $trait_i$ is the mean trait value of the species i, p_i is the proportion (biomass) of the species i in the community, and n the number of species in the community. In this study, the SLA, LDMC and DMC stand for the community-weighed means of the traits in each community.

Root sampling and trait measurements

After aboveground biomass sampling, two soil cores were collected in each quadrat (8 cm diameter, 1 m depth). The two soil cores were divided into 5 layers corresponding to the following depths: 0–10 cm, 10–20 cm, 20–40 cm, 40–60 cm, 60–100 cm. Then, each layer of the soil cores was vertically cut in half. For each quadrat, two halves originating from the same layer but from different soil core were combined for root measurements, and the two other halves were combined for water content measurements. All the samples were stored in a freezer at −20 °C before root measurements. After storage, the samples were thawed out in water. Roots were washed and separated into herbaceous roots and grapevines roots. Grapevines roots were not included in the analysis, as we hypothesized that grapevines transpiration was null or low at budburst. Subsamples of herbaceous roots were put in a clear acrylic tray with water, and roots were scanned at 600 dpi (scanner Epson Perfection V800). The software WinRHIZO Reg (Regent Instruments, Quebec, Canada) was used to analyze scanned images. As we were not able to differentiate root orders in the soil cores (McCormack et al. 2015), diameter classes were used to sort out the roots: each 0.1 mm from 0 to 1 mm, each 0.5 mm from 1 to 2 mm and the class >2 mm. Over all plant communities, roots <2 mm represented systematically between 98% and 100% of the total root length of each community, so all roots were included in the analysis. The software analysis calculates the surface area, mean diameter, volume and total length of the scanned roots, and the total length for each diameter class. Scanned samples were oven dried (60 °C, 72 h) and weighted, as were the non-scanned samples.

The roots of the various herbaceous species composing the communities couldn't be differentiated, so "root functional markers" of the communities (Damour et al. 2015) were calculated instead of functional traits of the species separately (Violle et al. 2007). These markers

Table 1 Description of the three soil management strategies applied in the inter-rows before the sowing of service crops in September 2016

Soil management strategy	2012–2013	2013–2014	2014–2015	2015–2016
SC	*Festuca sp. +Lolium perenne*	*Festuca sp. +Lolium perenne*	*Hordeum vulgare*	*Vicia faba*
SCT	*Festuca sp. +Lolium perenne*	*Festuca sp. +Lolium perenne*	*Hordeum vulgare*	Tillage
T	Tillage	Tillage	Tillage	Tillage

SC previous service crop, *SCT* previous service crop + tillage, *T* tillage alone represent the root traits of an "average plant" representing the community, as for aboveground traits (Garnier et al. 2004; Ricotta and Moretti 2011). Root functional markers were first calculated for each soil layer. Total root length was calculated with scanned length and biomass, and non-scanned biomass. Root mass density (RMD, kg m^{-3}) and root length density (RLD, cm cm^{-3}) were calculated as total root biomass and length divided by soil volume, respectively. Mean diameter (DIAM) was calculated by the software, specific root length (SRL, m g^{-1}) was calculated dividing root length by root dry mass, and very fine root fraction (VFRf) as the length of roots <0.1 mm divided by total root length. To account for differences in trait values between shallow and deep layers, and associated rooting strategies of plant communities (Fort et al. 2017), we calculated shallow markers by averaging the root functional markers of the topsoil layers (0–10 cm and 10–20 cm) and deep markers by averaging the root functional markers of the deep soil layers (40–60 cm and 60–100 cm). Finally, root mass fraction (RMF) was calculated as the total root biomass divided by the total community biomass (aboveground and belowground).

Indicators of runoff mitigation and water provisioning

The cover rate was chosen as the indicator of runoff mitigation. To assess the potential of erosion control of the service crops, we consider a soil is in a favorable condition based on the minimal threshold found in the literature corresponding to a soil cover of 40%. As grapevines root depth was not measured in our experiment, we couldn't calculate the TTSW nor FTSW of the grapevine in our experiment. Instead, we calculated the total water stock at 1 m depth at grapevines budburst as the indicator of water provision:

$$WS = WC*D*(100-GC) \times BD \times 10^{-4} \tag{2}$$

with WS the water stock (mm), WC the gravimetric soil water content (%), D the thickness of the soil layer (mm), GC the gravel content (%, in mass) and BD the bulk density of the soil layer (g cm^{-3}). We hypothesized that the water stock is well correlated with the ASW for grapevines due to soil homogeneity in our experimental field. However, it is difficult to assess absolute water availability at this stage without information on the grapevine TTSW. Moreover, rainfall may occur later in the season, and recharge the soil water and compensate for water deficit at budburst. For these reasons, we hypothesized that the higher the soil water content at budburst, the lower the risk of water stress would be within grapevines cycle, making the management of the service crop to avoid yield losses easier. The mean soil water stock value at budburst within our dataset was focused on to separate the more "favorable" and "unfavorable" water stocks in this study.

Soil water provisioning measurement

In all quadrats and for each soil layer, the two soil core halves that were not used for root measurements were combined and a sub-sample of soil was weighted to determine the soil fresh mass. Then, samples were oven dried (103 °C, 72 h), and weighted to determine their dry mass. After measuring the dry mass, samples were put in a sieve (2 mm) in water to separate the soil from the gravels. Gravels were then oven dried (103 °C, 24 h) and weighted. For each soil layer, gravimetric water content was then calculated following the equation

$$WC = \frac{FM-DM}{DM-GM} \times 100$$

where WC is the gravimetric soil water content (%), FM the soil fresh mass (g), DM the soil dry mass (g), and GM the mass of gravels (g).

Total soil water stock was calculated by aggregating the water stock of each soil layer. However, to avoid taking into account the excessive moisture in the two topsoil layers (0–10 cm and 10–20 cm) due to recent rainfall before sampling, the total water stock was calculated between 20 cm and 100 cm depth. Additionally, the water stock was measured on 5 tilled inter-rows (bare soil) as controls to assess the relationship between water stock and cover rate.

Data analysis

In this study a linear regression analysis was performed on the whole dataset to assess the relationship between vegetation cover rate and soil water stock. Relationships between functional markers were assessed using a calculation of correlations, principal component analysis (PCA) and Hierarchical Ascendant Classification (HAC). The HAC helps to emphasize functional groups among plant communities, and then compare indicators of service provision of each group. Because of the unbalanced combination of service crop x soil management treatments, regression analyses along functional gradients were used to quantify trade-off or synergies between traits and ecosystem services.

Differences between shallow and deep root markers were assessed with Wilcoxon signed rank test. Then Spearman correlations between each pair of functional markers were calculated. Spearman correlations are based on ranks so as to avoid over-weighting issues from outliers. Moreover, it allows the inclusion of variables that are not gaussian to be used in calculations. After data standardization, a PCA was then performed on the functional markers that showed significant correlations with the water stock and the cover rate. Following PCA, clusters were identified using a hierarchical ascendant classification (HAC) based on Ward criterion and followed by a K-means consolidation (Lê et al. 2008; Husson et al. 2017). The dominant botanical family of each quadrat was included as an illustrative variable in the classification. Significant differences between clusters were assessed with Kruskal-Wallis test and Fisher's least significant difference, with a *p*-values adjustment based on Holm method. This test was performed with the *kruskal* function from R package *agricolae* (de Mendiburu 2017). For illustrative variables (i.e. dominant family and soil management strategy), a v-test was performed to assess the relationship between qualitative variables and the clusters, then each cluster is compared with the whole dataset to assess for significant differences (Husson et al. 2017). HAC and v-test were performed with the *FactoMineR* package (Lê et al. 2008). Moreover, we focused on the functional markers of three communities from each cluster, originating from the same soil management strategy (SC), to confirm HAC results.

To assess the relationships between functional markers and indicators of service provision, we performed multiple regressions between indicators of service provision and the functional markers that showed significant correlations with the two indicators of service provision. We performed stepwise backward selection based on AIC criterion to identify best models, and assess the significance of particular functional markers in the models. In addition, relative contributions of the functional markers in the final models were calculated based on R^2 partitioning: we use the R package *relaimpo* and the recommended method LMG (Grömping 2006). All functional markers were included in initial models, then we calculated the variance inflation factor (VIF) to detect colinearity problems and remove redundant markers before model selection. Significance of functional markers was tested with an analysis of variance and type II sum of squares using *Anova* function from R package *car* (Fox and Weisberg 2011). All statistical analysis was performed with R (R Core Team 2018).

Results

Trade-off between services indicators

A significant negative relationship was found between water stock at budburst and the service crop cover rate ($\alpha = 0.05$), highlighting a trade-off between the two services (Fig. 2). Cover rate values ranged from 27% to 100%, with a mean value of 65% and a coefficient of variation of 36%. Over all quadrats, 84% had a cover rate > 40%. Water stock values ranged from 139 to 228 mm, with a mean value of 183 mm. When considered in relation to the threshold level of cover recommended to reduce runoff and the mean water stock, 75% of the quadrats had a cover rate value greater than 40%, and 61% of the quadrats were above the mean water stock. However, the cover rates and soil water stocks also depended on the soil management strategy: SC showed higher cover rates than SCT and T (Fig. 2, Kruskal-Wallis test, $\alpha = 0.05$).

Functional diversity of service crop communities

For all root markers, differences between shallow and deep markers were significant ($p < 0.05$ for all markers). SRL_{sh} and VFR_{sh} were higher than SRL_{dp} and VFR_{dp}, respectively, while $DIAM_{dp}$ was higher than $DIAM_{sh}$. For the density markers RMD and RLD, values were systematically higher in shallow layers than deep layers (Table 2). Regarding to the coefficient of variation, root functional markers were more variable than aboveground markers (Table 2).

Root mean diameter (RMD) was negatively correlated with specific root length (SRL) and very fine root fraction (VFR) (Fig. 3, Fig. S1, Table S4). Communities exhibiting high SRL had low root length and mass density in deep soil layers, while root diameter was positively correlated to rooting depth (Fig. 3, Table S4). Communities exhibiting high aboveground dry matter contents tended to be shallow rooted.

Fig. 2 Relationship between the soil water stock (mm, 1 m depth) and the cover rate (%) at grapevines budburst for all quadrats. Dashed black line represents the linear regression between water stock and cover rate showing a trade-off between the two indicators. Dotted gray lines indicate thresholds that were focused on to assess the quality of service provision (40% cover rate, mean water stock within the dataset)

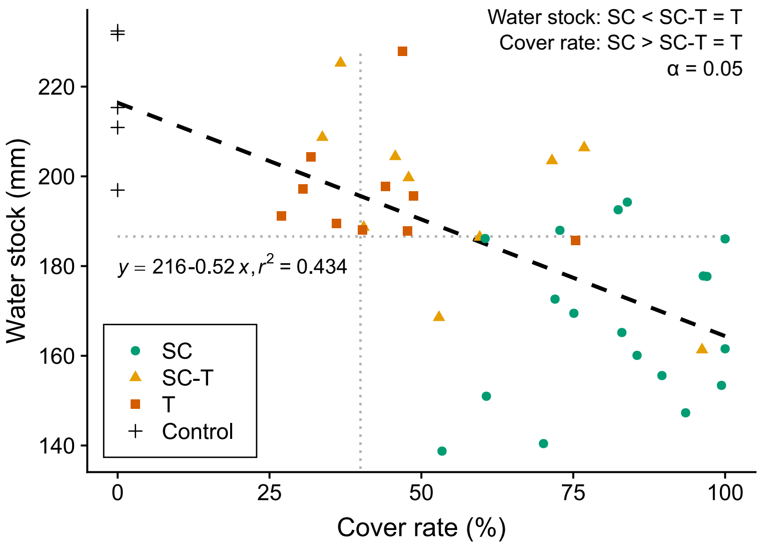


Table 2 Functional markers means, standard deviations, minimum and maximum values, and coefficient of variations of all service crop communities. Aboveground markers correspond to CWM calculations, belowground markers were directly measured at community scale

Functional markers	Mean	Std dev.	Min	Max	CV (%)
DMC (mg g^{-1})	155	20	105	198	13
LDMC (mg g^{-1})	165	22	109	215	14
SLA (m2 kg^{-1})	15.7	4.0	8.4	25.4	26
DIAM$_{\text{sh}}$ (mm)	0.19	0.04	0.13	0.26	20
DIAM$_{\text{dp}}$ (mm)	0.29	0.03	0.22	0.39	11
RLD$_{\text{sh}}$ (cm cm^{-3})	13.0	5.3	4.2	27.0	41
RLD$_{\text{dp}}$ (cm cm^{-3})	0.57	0.37	0.11	1.53	67
RMD$_{\text{sh}}$ (kg m^{-3})	0.60	0.24	0.25	1.31	40
RMD$_{\text{dp}}$ (kg m^{-3})	0.04	0.02	0.01	0.098	62
SRL$_{\text{sh}}$ (m g^{-1})	290	92	145	446	32
SRL$_{\text{dp}}$ (m g^{-1})	170	31	105	273	18
VFR$_{\text{sh}}$	0.40	0.13	0.20	0.67	32
VFR$_{\text{dp}}$	0.16	0.05	0.07	0.30	32
RMF	0.37	0.11	0.07	0.56	31
D80 (cm)	17	8	6	40	49

DMC dry matter content, *LDMC* leaf dry matter content, *SLA* specific leaf area, $DIAM_{sh}$ shallow mean root diameter, $DIAM_{dp}$ deep mean root diameter, RLD_{sh} shallow root length density, RLD_{dp} deep root length density, RMD_{sh} shallow root mass density, RMD_{dp} deep root mass density, SRL_{sh} shallow specific root length, SRL_{dp} deep specific root length, VFR_{sh} shallow very fine root fraction, VFR_{dp} deep very fine root fraction, *RMF* root mass fraction, *D80* depth of 80% of root length

Specific leaf area (SLA) wasn't correlated to any other aboveground functional marker, and was positively and negatively correlated with root diameter and VFR, respectively (Table S4). The communities exhibiting high dry matter content, SRL and VFR had low cover rate, whereas root diameter was positively correlated with the cover rate, along with deep root densities (RLD and RMD) and rooting depth. Soil water stock was positively correlated with aboveground dry matter contents, and negatively correlated with deep root density and rooting depth (Table S4).

The PCA explained 71.2% of total variance within the two first axes (Fig. 3a). First axis explained 50.1% of total variance with main contributions from morphological root functional markers VFR$_{\text{sh}}$, SRL$_{\text{sh}}$ and DIAM$_{\text{sh}}$ (Fig. 3a, Fig. S1). The second axis explained 21.1% of total variance and opposed communities by their rooting depth and length density in deep soil layer (Fig. 3a, Fig. S1).

The hierarchical ascendant classification resulted in three clusters (Fig. 3b). Cluster 1 was dominated by Boraginaceae and Poaceae species, with an absence of dominant Fabaceae species in the communities (Table 3). Communities were characterized by high plant dry matter content (DMC), fine roots, and low rooting depth (Fig. 3b, Table 3), and mainly originated from the T (tillage) soil management strategy (Table 3, Fig. S2). Cluster 2 was dominated by Asteraceae species, and was characterized by thicker roots, a low rooting depth, and high plant dry matter content. Half of the communities from cluster 2 were in the soil management strategy SCT. Cluster 3 was largely dominated mainly by Fabaceae

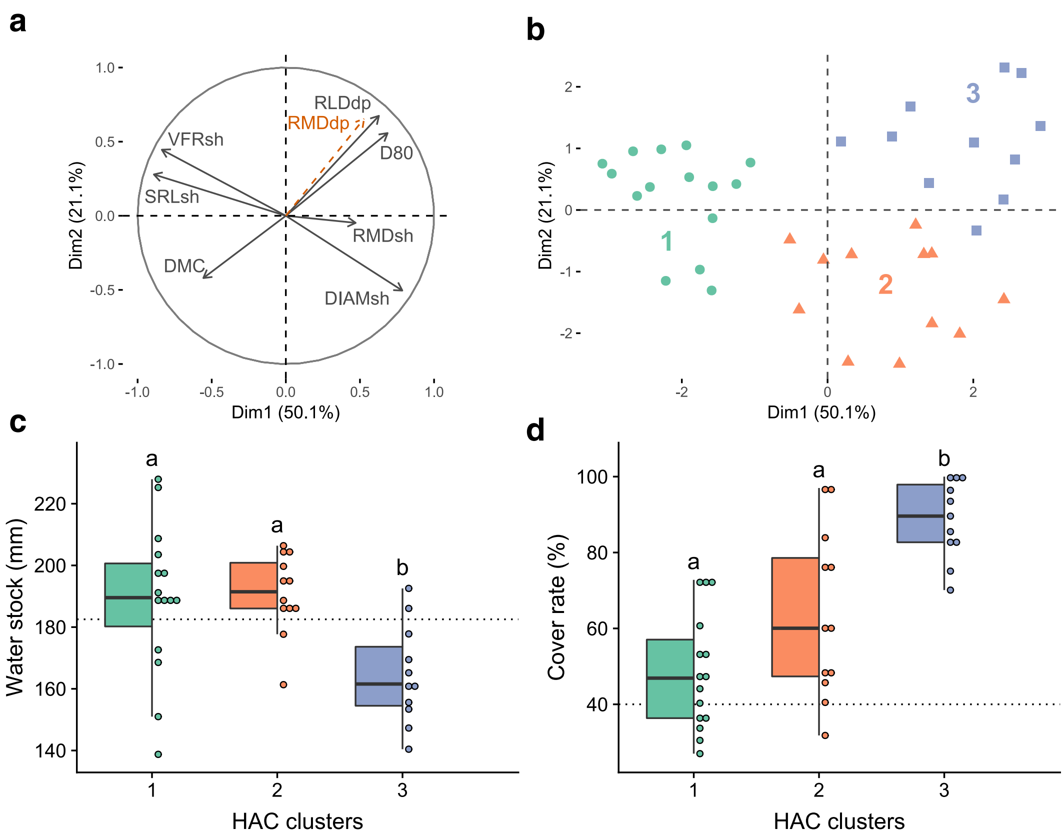


Fig. 3 Principal component analysis (PCA) between functional markers of the 38 communities. **a** PCA variables graph (see Table 1 for abbreviations of variables); **b** PCA individuals graph. Point shape and color indicates the three clusters built using a Hierarchical Ascendant Classification (HAC). **c** Boxplots and point data of soil water stocks (1 m depth) of the three clusters from HAC. Different letters indicate significant differences (Kruskal-Wallis test, $p < 0.05$). Dotted line illustrates the overall mean soil water stock. Point data were rounded at 2 mm in this graph. **d** Boxplots and point data of the cover rates of the plant communities, for each cluster from HAC. Different letters indicate significant differences (Kruskal-Wallis test, $p < 0.05$). Dotted line illustrates a 40% threshold for cover rate. Point data were rounded at 2% of cover rate in this graph

and some Plantaginaceae species, characterized by thick roots, deep and dense root systems, and low plant dry matter content (Fig. 3b, Table 3). All the communities from cluster 3 were in soil management strategy SC (Table 3, Fig. S2).

Relationship between functional markers and indicators of service provision

Cluster 3 showed the lowest water stock values, with a mean of 164 mm (Fig. 3c-d, Table 3). Cluster 1 and 2 had significant higher values of soil water stock than cluster 1, with mean values of 189 and 191 mm, respectively. Comparing with the mean soil water stock within our dataset, only 18% of quadrats from cluster 3 were above the mean, while 73% and 83% of quadrats from cluster 1 and 2, respectively, were above the mean (Fig. 3c). Regarding to the cover rate, cluster 3 had the highest values, with a mean of 89%. Cluster 1 and 2 showed lower values of cover rate but were not different between each other (Fig. 3c-d, Table 3).

When the analysis was constrained to plots that have had service crops sown since 2012 (SC), the previous soil management with the most consistent emergence of the experimental service crops, there were clear patterns in functional markers between clusters (Fig. 4). Pattern of DMC variation between clusters confirmed observations on the whole dataset, with low DMC values in cluster 3. The communities sown with *Plantago coronopus* (Pc3, Table S1 and S3) and *Vicia villosa* (Vv2, Table S1 and S3) showed the lowest DMC values. The community sown with *Medicago lupulina* (Ml3, Table S1 and S3) had the highest DMC value (Fig. 4). The communities sown with *Phacelia tanacetifolia* and

Table 3 Differences between clusters: functional marker of the PCA and indicators of service provision (mean ± standard deviation), and results of the v-test performed in HAC for the variable "dominant family"

	C1	C2	C3
D80 (cm)	12.47 ± 4.54 ***a***	13.95 ± 4.91 ***a***	27.99 ± 6.2 ***b***
$DIAM_{sh}$ (mm)	0.15 ± 0.01 ***a***	0.22 ± 0.03 ***b***	0.2 ± 0.03 ***b***
DMC (mg g^{-1})	187.88 ± 14.62 ***a***	181.28 ± 18.86 ***a***	157.34 ± 20.08 ***b***
RLD_{dp} (cm cm^{-3})	0.34 ± 0.16 ***a***	0.42 ± 0.18 ***a***	1.03 ± 0.35 ***b***
RMD_{dp} (kg m^{-3})	0.03 ± 0.02 ***a***	0.03 ± 0.02 ***a***	0.07 ± 0.02 ***b***
RMD_{sh} (kg m^{-3})	0.45 ± 0.17 ***a***	0.75 ± 0.26 ***b***	0.65 ± 0.19 ***b***
SRL_{sh} (m g^{-1})	388.47 ± 43.23 ***a***	220.01 ± 57.27 ***b***	233.35 ± 41.38 ***b***
VFR_{sh} (%)	0.52 ± 0.09 ***a***	0.3 ± 0.07 ***b***	0.34 ± 0.08 ***b***
Dominant family	Boraginaceae (+) (21.4%) Poaceae (+) (42.9%) Fabaceae (−) (0%)	Asteraceae (+) (33.3%)	Fabaceae (+) (63.6%) Plantaginaceae (+) (27.3%) Poaceae (−) (0%)
Soil management	T (+) (46.7%) SC (−) (26.7%)	SCT (+) (50%)	SC (+) (100%) SCT (−) (0%) T (−) (0%)
Water stock (mm)	189 ± 24 ***a***	191 ± 13 ***a***	164 ± 16 ***b***
Cover (%)	48 ± 15 ***a***	64 ± 22 ***b***	89 ± 10 ***b***

The test compares the cluster values to the overall values. A (+) sign indicates that the cluster values are higher than the overall values, a (−) sign indicates that the cluster values are lower than the overall values (Chi-2 test). Different letters indicate significant differences between clusters (Kruskal-Wallis test). C1, C2 and C3 indicate cluster 1, cluster 2 and cluster 3, respectively. See Tables 1 and 2 for abbreviations of variables

Plantago coronopus (Pt3 and Pc3) exhibited the lower SLA whereas communities sown with *Medicago lupulina* and *Vicia villosa* (Ml3 and Vv2) exhibited the highest SLA values (see Table S1 and S3 for details on communities' species abundance).

Regarding to the root functional markers, differences were more pronounced and confirmed the results highlighted in Table 3. Indeed, the communities of clusters 2 and 3 had a higher root diameter ($DIAM_{sh}$) and a lower SRL_{sh} than communities of cluster 1, and communities dominated by Fabaceae species had the highest root diameters. Moreover, the cluster 3 had a higher mean rooting depth and deep root density than the two other clusters, although it depended on communities (Fig. 4).

Communities sown with *Medicago lupulina*, *Vicia villosa* and *Trifolium fragiferum* (Ml3, Vv2 and Tf3 in Fig. 4) showed the highest soil cover rates among the 9 communities originating from the SC soil management strategy, with values between 90% and 100%. Communities sown with *Achillea millefolium* and *Plantago coronopus* also had high cover rates, between 80% and 90%. Overall, the 9 SC communities had cover rates higher than 60% of cover. Regarding to the soil water stock, communities from cluster 2 had higher mean values. The three communities from cluster 3 had the lowest water stock values. Among the 9 SC plant communities, the communities sown with *Medicago lupulina* and *Achillea millefolium* showed an interesting trade-off between the soil coverage and the water stock.

Over all fitted models, adjusted R^2 ranged from 0.37 to 0.87, and all functional markers were significant (Table 4). The nature and number of functional markers remaining in the best models depended on the soil management strategy, and the indicator of service provision. Regarding to the water stock, the 'fine root' functional markers (SRL, VFR) were negatively related to the soil water stock, except for VFRdp which had a positive effect on the soil water stock in the soil management strategy T (Table 4). Moreover, plant dry matter content (DMC) was positively related to soil water stock in soil management strategy SCT, and shallow root length density (RLDsh) was positively related to the soil water stock in soil management SC. Regarding to the soil cover, the DMC was negatively related to the cover rate in soil management strategy SC, while the SLA was positively related to the cover rate in soil management strategies SC and SCT (Table 4). Deep

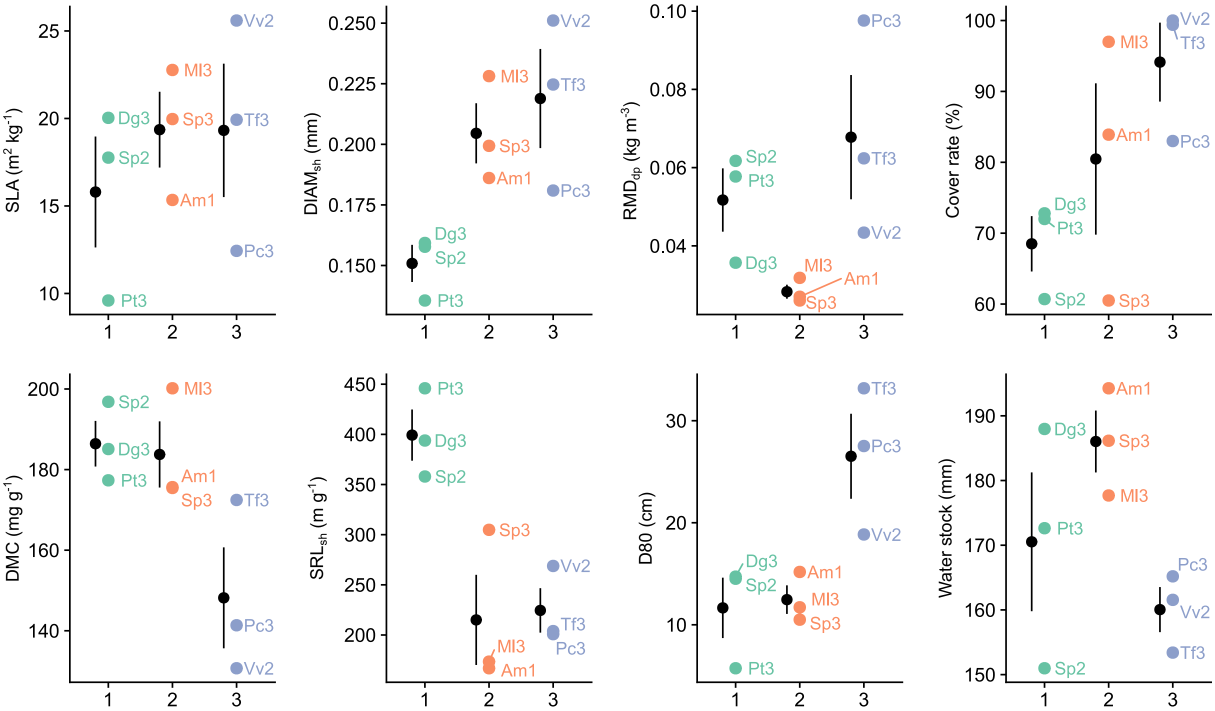


Fig. 4 Indicators of service provision (cover rate and water stock) and functional markers of communities from the three clusters, sampled in the same soil management strategy (SC). Black points with ranges illustrate the mean and standard error. See Table S1 for abbreviations, Table S1 for quadrat codes

root length density (RLDdp) was positively related to the cover rate in soil management SCT. The shallow and deep very fine root fraction were positively and negatively related to the cover rate in the soil management strategy SC, respectively, while deep specific root length (SRLdp) was negatively related to the cover rate in soil management strategy T.

Discussion

Covariations between indicators of service provision and within community functional markers

The two indicators of service provision showed a trade-off between runoff and erosion control and water provisioning (Fig. 2). Although a cover crop may increase water infiltration during the winter (Gaudin et al. 2010) it will also consume this additional water and may dry out the soil profile before grapevines budburst (Celette et al. 2008). We were, therefore, interested in optimizing the functional composition of the service crop to balance these two services.

Results from correlations and PCA confirm previous evidence of a root economics spectrum discriminating between species or communities having acquisitive traits, i.e. fine roots, high specific root length (SRL) and very fine root fraction (VFR), from those having conservative traits, i.e. thick roots, low SRL and VFR (Prieto et al. 2015; Reich 2014; Roumet et al. 2016, Fig. 3a, Table 2). Moreover, morphological root markers varied with the soil depth: SRL and VFR were higher in shallow layers compared to deep layers, while root diameter was higher in deep layers. These findings confirm previous results suggesting that shallow roots have a more acquisitive strategy compared to deep roots (Prieto et al. 2015; Fort et al. 2016). Large diameter in deep layers is related to water acquisition and transport to aboveground organs (Hernández et al. 2010; Comas et al. 2013; Fort et al. 2017).

The relationships between root length density (RLD), root mean diameter and very fine root fraction (VFR) are consistent with the fact that species with a fine rooting strategy (high VFR and SRL) produce root length faster than species exhibiting

Table 4 Summary of the models between functional markers and indicators of service provision after variable selection procedure, for each soil management strategy

	Water stock					Cover rate				
	Functional markers	Estimates	Contrib	adj.R^2	p.value	Functional markers	Estimates	Contrib	adj.R^2	*p* value
SC	SRLdp	−12.7	0.17	0.37	0.0226	DMC	−6.8	0.17	0.81	0.0001
	VFRsh	−14.01	0.39			SLA	6.2	0.18		
	RLDsh	16.9	0.44			VFRsh	−6.1	0.26		
						VFRdp	12.3	0.23		
						D80	3.6	0.17		
SCT	DMC	12.2	0.51	0.75	0.0031	SLA	17.9	0.53	0.62	0.0134
	D80	−17.1	0.49			RLDdp	27.7	0.47		
T	VFRdp	8.5	1	0.65	0.0051	DIAMsh	11.6	0.29	0.87	0.0009
						SRLdp	−17.2	0.71		

The variables that were retained in the final model are indicated with their estimate, relative importance in the model, and *p* value. Estimate: partial slope for each of the functional marker; Contrib: relative contribution of each functional marker. All included markers were significant in each model. *SC* previous service crop, *SCT* previous service crop + tillage, *T* tillage alone

large roots, and exhibit higher RLD (Table 2, Eissenstat 1992). High SRL is often exhibited by thin roots with low root dry matter content and low tissue density (Prieto et al. 2015; Roumet et al. 2016), resulting in this experiment in low root mass density (RMD, Table 2). Surprisingly, we didn't find any correlation between plant or leaf dry matter content (DMC and LDMC), and SLA. Both SLA and LDMC are key traits of the leaf economic spectrum, the latter being closely related to the leaf life span (Kazakou et al. 2006, 2009; Garnier et al. 2007). At community level, correlations between SLA and LDMC have been found with studies on gradients of resources, soil types, field ages and woody species (Garnier et al. 2004; Pérez-Ramos et al. 2012). However, Tribouillois et al. (2015b) measured the functional traits of 36 service crop species and found no relationship between SLA and LDMC. In our study, native weeds were abundant in some of the plant communities (Table S1) and may have been filtered by a common environment so as to present lower trait variance and closer mean values of above ground traits (Violle et al. 2012). This may have masked the a priori functional diversity introduced with the sown species (Damour et al. 2018). In addition, human selection of cultivated species (i.e. most of the sown species) had maximized the light acquisition potential of plants, and may have dampened the functional trade-offs that are often observed in non-cultivated species.

Relationships between soil management strategies and indicators of service provision

The soil management strategy was clearly related to the indicators of service provision, as revealed by the PCA and cluster analysis (Fig. 2, Fig. S1). However, we were not able to analyze further the effect of soil management strategies on the functional structure of plant communities, due to emergence problems leading to an unbalanced experimental design between sown species and soil management strategies (Table S1). The relationship between the two indicators and the soil management strategy seemed partially due to its influence on service crops establishment. Indeed, all the communities in the cluster 3 originated from the soil management strategy SC (Table 1), and had the lowest water stock and the highest cover rate (Fig. 2, Fig. 3, Table S4). In contrast, communities from the soil management strategy T had the highest water stock and the lowest cover rate; the communities from the soil management strategy SCT (Table 1) had intermediate water stock and cover rate values (Fig. 1). Maintaining service crop practices over several years (Table 1) may have improved soil quality (Salomé et al. 2016), resulting in better emergence conditions for service crops, and a higher soil cover than in tilled soils. However, a higher soil cover may increase transpiration fluxes and decrease the soil water stock (Fig. 1). In this study we observed service crop communities that had both high cover rate and water stock, and we need to look further to bring some insights regarding the relationships between communities' functional markers and the indicators of service provision.

Relationships between functional markers and indicators of service provision

One objective of this study was to identify the functional makers that were related to the total soil water stock and the cover rate of service crops, indicators of water provision and runoff control. In this study, we chose to assess the relationships between the indicators of service provision and the mean values of functional markers (CWM), and we didn't include indicators of functional variability as the measure of functional diversity (Laliberte and Legendre 2010), community-weighed variance, kurtosis or skewness (Gross et al. 2017), and didn't focus on intraspecific variability (Violle et al. 2012; Siefert et al. 2015). We assume this choice as we first wanted to assess relationships between commonly used indicators before integrating more complexity, but we are aware that it could limit our results. Indeed some authors recently revealed the importance of diversity per se in driving ecosystem functions (Li et al. 2014; Zemunik et al. 2015; Siefert et al. 2015; Gross et al. 2017), but that is not always the case (e.g. Barkaoui et al. 2016). However, in this study, the comparison of functional groups originating from the same soil management strategy (Table 3, Fig. 4) and the model selection procedure (Table 4) confirmed the potential of trait-based approach to study service provision by service crops in agriculture (Cresswell et al. 2019).

Aboveground functional markers Our results showed that plant dry matter content (DMC) and specific leaf area (SLA) were related to the indicators of services provision linked to the water balance of the soil vineyard. The DMC was negatively related to the cover rate in soil management strategy SC and positively related to the soil water stock in the soil management strategy SCT (Fig. 3, Fig. 4, Table 3, Table 4). Moreover, SLA was positively related to the cover rate in the soil management strategies SC and SCT. These results agree with ecological theory as high dry matter contents are exhibited by resource-conservative species that deplete water slower than resource-acquisitive species, which generally exhibit higher SLA than the former (Reich et al. 2003; Díaz et al. 2004, 2016; Reich 2014). Previous findings suggest that LDMC could be robust to highlight plant strategies (Garnier et al. 2001; Roche et al. 2004; Al Haj Khaled et al. 2005; Kazakou et al. 2009). Our results indicated that the DMC was the best functional marker explaining water stock variations at community level including sown species (Table 4).

Rooting depth and density Density-related functional markers, i.e. root length density (RLD) and root mass density (RMD) are dependent on the growth differences between communities, related to the soil conditions in which they grow, and the other species in competition for resources (Craine 2006). In this experiment, the communities that exhibited deep root systems (D80), high root length density (RLD) and mass density (RMD) in the deep soil layer showed the lowest water stocks and higher cover rates (Fig. 3, Table S4). Moreover, D80 and DMC explained 75% of the water stock variance in the soil management SCT, while RLDdp and SLA explained 62% of cover rate variance in the same soil conditions (Table 4). This result was expected as root length and depth may be one of the most important traits related to water and nutrient acquisition (Eissenstat 1992; Violle et al. 2009; Freschet and Roumet 2017), and $\mathrm{RMD}_{\mathrm{dp}}$ was closely related to RLDdp in this experiment (Table 2, Fig. 3). Deep root system had access to more water, which probably explains the higher cover rates observed for these communities. The positive slope of RLDsh in the regression on soil water stock in the soil management strategy SC is surprising, and may find an explanation regarding to the morphological root traits exhibited by communities showing high RLDsh.

Morphological root functional markers The deep specific root length (SRLdp) and shallow very fine root fraction (VFRsh) were negatively related to the soil water stock in the soil management strategy SC (Table 4). Fine rooting strategy is positively related with resource acquisition as it allows a large soil exploration with a low carbon investment per root length (Reich 2014; Freschet and Roumet 2017; Fort et al. 2017). RLDsh was positively related to SRLdp and negatively related to deep root diameter (DIAMdp), which may explain its importance in the model SC (Table 4). However, the functional group exhibiting high SRL and VFR (cluster 1) also had shallower root systems and the highest water stocks, while cluster 3 exhibited high root diameter, deep root systems and low soil water stocks (Fig. 3, Table S4), contrary to expectations. Soil management strategies probably explain this observation:

the communities exhibiting fine roots were over-represented in the soil management strategy T (several years of soil tillage with no organic inputs), and species exhibiting acquisitive strategies may also be less tolerant to water or nutrient stress (Reich 2014; Isaac and Borden 2019). In addition, large root diameter in deep layers may favor water extraction and transport to the upper plant organs (Hernández et al. 2010; Fort et al. 2016, 2017). Eissenstat (1992) suggested that rates of water uptake can be higher in coarse roots of dicot species, compared to the fine roots of graminoid species. The results of the present experiment are consistent with these findings. Surprisingly, shallow and deep fine root fractions (VFR) had opposite effects on the cover rate in the soil management strategy SC. Among herbaceous, legumes exhibit thick roots (Roumet et al. 2008), and have a better ability to grow under low nitrogen content due to symbiotic fixation. This may explain the negative slope of VFRsh in the soil management strategy SC, and the positive slope of DIAMsh in the soil management strategy T (Table 4). The high proportion of fine roots in deep layer may have favored species development during a relatively dry winter and spring (Fig. 1), explaining the positive effect of VFRdp in the model (Table 4). In the soil management strategy T, SRLdp had a negative contribution in the regression on cover rate, suggesting that nitrogen was more limiting than water in these soil conditions.

Towards an ideotype of service crops based on functional markers to achieve both water refilling and runoff reduction?

Regarding the indicators of service provision, the focus on the communities originating from soil management strategy SC raised some interesting questions (Fig. 4). All the 9 SC communities had cover rates above 60%, regardless of the functional markers of the community. This suggests that functional differences between communities accounted less than soil management strategy in terms of determining the ability of the service crop to significantly reduce runoff and erosion (Fig. 1).

However, the communities sown with *Medicago lupulina*, *Vicia villosa* and *Trifolium fragiferum* (i.e. Ml3, Vv2 and Tf3), largely dominated by the sown species (Table S3), showed the highest cover rates and shared similar values of SLA and $\mathrm{DIAM}_{\mathrm{sh}}$, suggesting that functional markers were still important in differentiating the ability of service crops to establish in a vineyard. Moreover, the community Ml1, sown with *Medicago lupulina* (see Table S3 for details), reached a cover rate close to 50% (Table S1) although located on regularly tilled (soil management strategy T, Fig. S2), confirming that Fabaceae species were better at establishing in low-fertility soils, probably due to their symbiosis with nitrogen-fixing bacteria. On the other hand, the lowest cover rates were found in communities sown with Poaceae species in low-fertility inter-rows, after several years of tillage (Table S1, Fig. S2). The best water stock values were obtained with the communities sown with *Achillea millefolium* (Am1), *Dactylis glomerata* (Dg3) and the spontaneous vegetation (Sp3). The three communities had similar values of $\mathrm{RMD}_{\mathrm{dp}}$, D80 and DMC (Fig. S3), suggesting that rooting depth and plant dry matter content are key traits to explain water consumption by service crops. We also confirmed that previous soil management strategy (e.g. tillage or intercropping) had a direct impact on community aboveground development and rooting. Moreover, we showed that it is possible to reach interesting trade-offs between antagonist services with temporary service crops that grew in a short period. When choosing service crop species in vineyards, vinegrowers should take into account their previous soil management practices as they also strongly influence service crop development and thus the services they may provide (Garcia et al. 2018).

Conclusion

In this experiment, we assessed the trade-off between the cover rate (considered as an indicator of runoff and erosion control) and soil water stock (water provision/retention) under an important number of functionally contrasting service crop communities, in different soil management strategies. We showed that both aboveground and belowground functional markers of service crops are significant indicators of service provision at the community level. Among them, the plant aboveground dry matter content positively related to soil water stocks and negatively related to the cover rate of the communities. Overall, the soil water stock was explained by root functional markers related to rooting depth and root morphology such as the very fine root fraction, specific root length and root mean diameter. These results agree with ecological theories about the relationships between plant functional markers, plant ecological strategies and resources use. The identification of functional markers related to service provision may help us to select species or communities service crops that could perform interesting trade-offs between multiple services due to a suited combination of related markers: in our Mediterranean conditions, *Medicago lupulina* (Fabaceae) seemed a good candidate as it exhibited high dry matter content, shallow rooting depth, and satisfactory water stock and cover rate values. The soil management strategies also influenced service crops establishment and thus service provision, which highlights the importance of developing long-term cover cropping practices and adaptive strategies regarding to the choice of service crop species, mixtures, and their associated functional structure to provide services. The identification of relevant combinations of functional markers related to ecosystem services could encourage screening programs for the identification of currently unknown species to provide ecosystem services (e.g. weed species), and thus enlarge the pool of species cultivated to provide agroecosystem services. Moreover, it may provide insights for plant selection, in order to breed plant varieties and cultivars with the aim of providing agroecosystem services.

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